IV.

AN ASEXUAL GROWTH FROM THE PROTHALLUS OF PTERIS SERRULATA.

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While studying the development of the archegonium in the Polypodiaceæ, a few weeks ago, in the botanical laboratory of the University of Strasburg, a peculiarity was first noticed in the prothallus of Pteris serrulata which seems to have an important bearing on the question of the fern prothallus in general.

The material used was taken from a pot in which Pteris serrulata and Aspidium molle had been sown. At the beginning of the investigation there were a number of seedlings of both the above-named species which were considerably advanced in growth; and in addition there were numerous prothalli, from some of which young plants had begun to grow, and others still younger on which no incipient plantlets could be discovered with the naked eye. A search was made among the latter for prothalli in a condition suitable to demonstrate the earliest stages of growth after the fertilization of the archegonium. Some of these prothalli were normally developed, having both antheridia and archegonia, from which occasionally an embryonal growth was seen. During the search, however, numerous specimens were found presenting the anomaly of scalariform ducts in the substance of the prothallus; and such prothalli, when still further developed, showed that the young fern-plantlets produced by them were the result of a direct budding of the cells, and not of the changes caused by the act of fertilization in a single embryonal cell. The number of cases in which the above-mentioned peculiarity was manifested was about fifty; but, undoubtedly, the actual number was greater, inasmuch as some of the young fern-plantlets in the pot, which were too old to allow one to say whether they were of the regularly developed (that is, by growth of an embryo) or not, probably belonged to the number of those developed by direct budding. The shape of the prothalli was, as usual, more or less obcordate; and those in which the anomaly presented itself, although variable in outline, were narrower than the

others. This narrowness may have been only accidental and the result of crowding in the pot, as very often happens in the cultivation of ferns. In a single case, Fig. 13, one side was developed into a sort of secondary prothallus. The cells of the prothalli were perhaps somewhat paler than usual; and those which, near the concavity of the heart, are generally more numerous than in other portions and isodiametrical, were here much longer than broad, — that is, longer in the direction from the centre of the prothallus towards the concavity. As is well known, fern prothalli are generally heart or kidney-shaped, and the two sides composed of a single layer of polygonal cells, the centre of a portion decidedly thicker and consisting of several layers, which we may call the cushion; and in this last-named portion are situated the archegonia, while the antheridia are much more widely dispersed, being found also in the lateral lobes. As before said, the most striking feature of the abnormal prothalli was the presence of a dotted duct in the cushion a short distance back of the concavity, just where the archegonia are generally found. But wherever such scalariform vessels were present there were no traces whatever of archegonia to be found, although antheridia were always abundant, as well as the hairs, which here fulfil the offices of roots. See Figs. 1, 6, and 9, in which *a* shows the position of the scalariform ducts. As may be seen from Figs. 6 and 9, the scalariform ducts arise singly, and are situated in the central portion of the prothallus. They scarcely differ in shape at first from the adjoining cells, which are longer and relatively narrower than the superficial cells. The ducts increase by division in a direction parallel to the surface, so that, in a longitudinal section, we find several lying one above the other.

Another peculiarity often, but not always, accompanying the presence of scalariform ducts, was the formation of a process or outgrowth in the concavity of the thallus, as shown in Figs. 1, 6, and 12. This outgrowth was variable in length, often being short and imbedded between the lateral lobes, but sometimes projecting as a narrow tapering process. In one case, it was forked at the extremity. The growth by means of a single terminal cell is shown in Fig. 3. As just mentioned, the existence of a process in the concavity is a striking peculiarity, but not quite a constant occurrence, as is the presence of scalariform ducts. The first scalariform duct arises in the prothallus, as I have just remarked; and soon appear others, always in a line between the original duct and the nearest point of the concavity. In this way arises an interrupted row of ducts, which may extend, when a process is present, nearly to its extremity. The cells surrounding the original vessel

soon assume the form of vessels themselves, and thus a rudimentary bundle is formed. It happens rarely that two such scalariform ducts appear simultaneously in parts of the prothallus remote from one another. I only saw one such case, Fig. 13, *a* and *b*.

It now becomes necessary to consider the relation of the scalariform ducts to the other cells of the prothallus, and this must be done by making longitudinal and transverse sections of the region in which the ducts lie. We have such longitudinal sections in Figs. 2 and 7, of which Figs. 1 and 6 give a view from above, but much less magnified. From these sections we see that the prothallus forms a compact tissue in which certain cells have assumed the character of scalariform ducts, while the others remain unchanged. From no section made was I able to see any trace of an archegonium. In two instances, when seen from above, a combination of four cells led me to suppose that there was some signification to be attached to this arrangement. Fig. 5 is a magnified view of Fig. 1, in which this arrangement in four occurs; but, as Fig. 4, a longitudinal section, shows no connection between the four surface cells and the scalariform ducts, I am compelled to regard the two cases mentioned as having only accidentally such a superficial cell-conformation.

So far the changes mentioned have taken place in the plane of the prothallus itself. Now a change occurs which produces a growth in a direction perpendicular to the prothallus, and this growth is easily distinguished from the usual embryo growth. A swelling is seen, generally on the under surface of the prothallus, shortly after the appearance of the scalariform duct. This swelling is situated on or very near the line connecting the original duct and the nearest point of the concavity. When there is a process, this swelling very often appears near its extremity, as in Fig. 6, *b*. When two such swellings appear simultaneously, they are generally situated side by side. In all cases, there is seen back of the swelling the scalariform duct or ducts lying in the substance of the prothallus itself. It is impossible for me to say in which cells of the prothallus this swelling or outgrowth originates. Longitudinal sections, as in Fig. 7, *a*, show no change by which the cells of the outgrowing portion — which is, in this case, on the upper instead of the lower surface of the prothallus, as is more commonly the case — can be distinguished from the cells which are to remain a portion of the prothallus. From the not unfrequent appearance of a bursting through the surface, it can perhaps be inferred that the superficial cells take no part in the growth. Certainly no particular cell or cells seem to be the place of origin of the new growth, but it seems to be a

direct continuation of the prothallus cells, and not a distinct organization temporarily attached to it, as is the case with an embryo growth. This swelling, to which I have intentionally avoided giving the name of bud, develops and shows all the characteristics of a fern leaf, and is, in fact, not a stem, but a true leaf. When it arises on the under surface of the prothallus, this leaf grows forwards, curves round the border of the concavity, and raises itself into the air. When two such swellings occur by the side of one another, one generally grows from the upper, the other from the under surface of the prothallus, as in Fig. 10. In the mean while, there appears on the basis of the leaf, or on what is now so far differentiated that it is evidently the leaf-stalk, a bud, which very soon can, by means of the cell-cap on its end, be recognized as a root. This grows always in a direction the reverse of the leaf; that is, backwards away from the concavity. After the appearance of the root, a bud appears on the basis of the leaf-stalk, looking towards the concavity, and from this grows the stem. As a rule, the leaf is tolerably far advanced in its development before the root appears, and the root invariably precedes the stem-bud. The terms forward and backward with relation to the concavity of the prothallus are, of course, inapplicable when the young plantlet is formed at or near the end of a process of the character above described, when the leaf and root shoot out *ad libitum*. In all cases a vascular bundle traverses the leaf and root, and these are in connection with the vascular bundle of the prothallus.

If now we compare Figs. 11 and 14, we shall clearly see that the cases we have been discussing differ widely from the ordinary cases of embryonal growth. Fig. 11 represents a longitudinal section through the spot where a young plantlet, such as we have described, shoots out from the prothallus (p, p,), b represents the leaf, r the root, and s the stem-bud, which was cut a little to one side of the median line. Fig. 14, taken from Sachs's Lehrbuch der Botanik, represents a longitudinal section of a prothallus and a normally developed embryo attached, the whole not so strongly magnified as Fig. 11. First, at a glance, 14 differs from 11 in the fact that the young plant in the latter case is so intimately connected with the prothallus that one cannot decide where the one begins and the other ends; while, in the former, it is perfectly easy to trace the outline of the young fern. Secondly, we have in 14 a structure known as the foot, f, by which the developing fern is separated from the prothallus, — a structure of which we find no equivalent in 11. Thirdly, the vascular bundle of the plantlet is in direct connection with vessels which lie wholly in the prothallus.

Fourthly, the order of evolution is different in the two cases. In 11, the leaf arose first, as we saw, and was tolerably well developed before a root and afterwards a stem-bud made their appearance. In 14 the root anticipates by far both the leaf and stem-bud in its development; and, in fact, the root and stem are not produced from the leaf-stalk, but (and this fact is not to be learned from the figure, but from the accompanying description in Sachs) by the subdivision of a single cell into four, one of which forms the foot.

So far as I know, a budding similar to that in the cases described is only mentioned by Wigand, "Botanische Zeitung," Feb. 16, 1849, and by him in language which, it must be confessed, is not a little obscure: "Eine beachtenswerthe Erscheinung begegnete mir bei einigen Exemplaren, nämlich eine *Sprossenbildung*, ungefähr an der Stelle des Lagers wo das beblätterte Pflänzchen angelegt wird, entspringen junge *Vorkeime* von derselben Gestalt, wie die Hauptvorkeime im jungen Zustande, mit dem verschmälerten Ende (dem Sporenende entsprechend), an dem Lager festsitzend, später sich loslösend und wie ein selbständiger Vorkeim sich verhaltend." From the above paragraph, it would be, perhaps, difficult to say whether Wigand had seen any thing similar to our case. But, taken in connection with his Tafel 1, Fig. 25, where a process in the concavity is clearly seen, it seems probable that he had seen a growth which did not proceed from a fertilized archegonium.

The bearing of the facts already enumerated upon the question of the function of the fern-prothallus is very important. Since the publication by Leszcyc-Suminski, in 1848, of his observations concerning the sexuality of ferns, the prothallus has been regarded as an organ intermediary between the spore and the fully developed plant, growing out of the former, and bearing sexual organs which by mutual co-operation produce the latter. It has been considered impossible for a spore to produce a fern-plant directly without the intervention of a sexual union. But, from the cases we have been considering, it is evident that this process is not absolutely necessary, since we have seen that a young fern can be produced from the spore by a purely vegetative or budding process, — a process as clearly unsexual as, for instance, the production of plantlets on the fronds of Asplenium viviparum. This fact is an unexpected one for those who constantly see unity and simplicity in nature. Although in by far the majority of cases the prothallus does bear archegonia whose embryos develop into ferns, the monstrosity, if so we please to call the present cases, having once been noticed, may of course be expected to occur at any time; and, now that the attention of botanists has been called to it, it may prove not to be rare. As, in the present

instance, certain examples bore archegonia with embryonal outgrowth, and others only direct bud-development, it is of course interesting to know whether the young plantlets of the two kinds of origin exactly resemble one another in their after development. For this purpose, a number of specimens evidently belonging to the category of abnormal growths were transplanted into a pot where their growth could be watched. So far there is no difference between their growth and that of plantlets developed from embryos.

In conclusion, I would take this opportunity to thank Professor De Bary of Strasburg for material and advice kindly afforded during the course of the foregoing investigations.

EXPLANATION OF THE FIGURES.

Figs. 1, 6, 9, 12, 13. Different forms of prothalli of Pteris serrulata, slightly magnified. In all, *a* represents the original scalariform duct; *b* the first leaf; *r* root; and *s* the stem-bud. In 12, *b'*, *r'*, *s'*, represent the corresponding parts of a second plantlet. In all, the position of the root-hairs and archegonia are seen in the lower part of the prothallus.

Fig. 2. A longitudinal section of fig. 1.

Fig. 3. View of a terminal growing cell of the same seen from above.

Fig. 4. Section parallel with *x*, fig. 3, and more highly magnified.

Fig. 5. A portion of fig. 1 seen from above; *a* original scalariform duct; *x* signifies the same cells as in 2 and 4.

Fig. 7. Longitudinal section of fig. 6, in which *a* represents the upward-growing portion. Several antheridia are seen at one end.

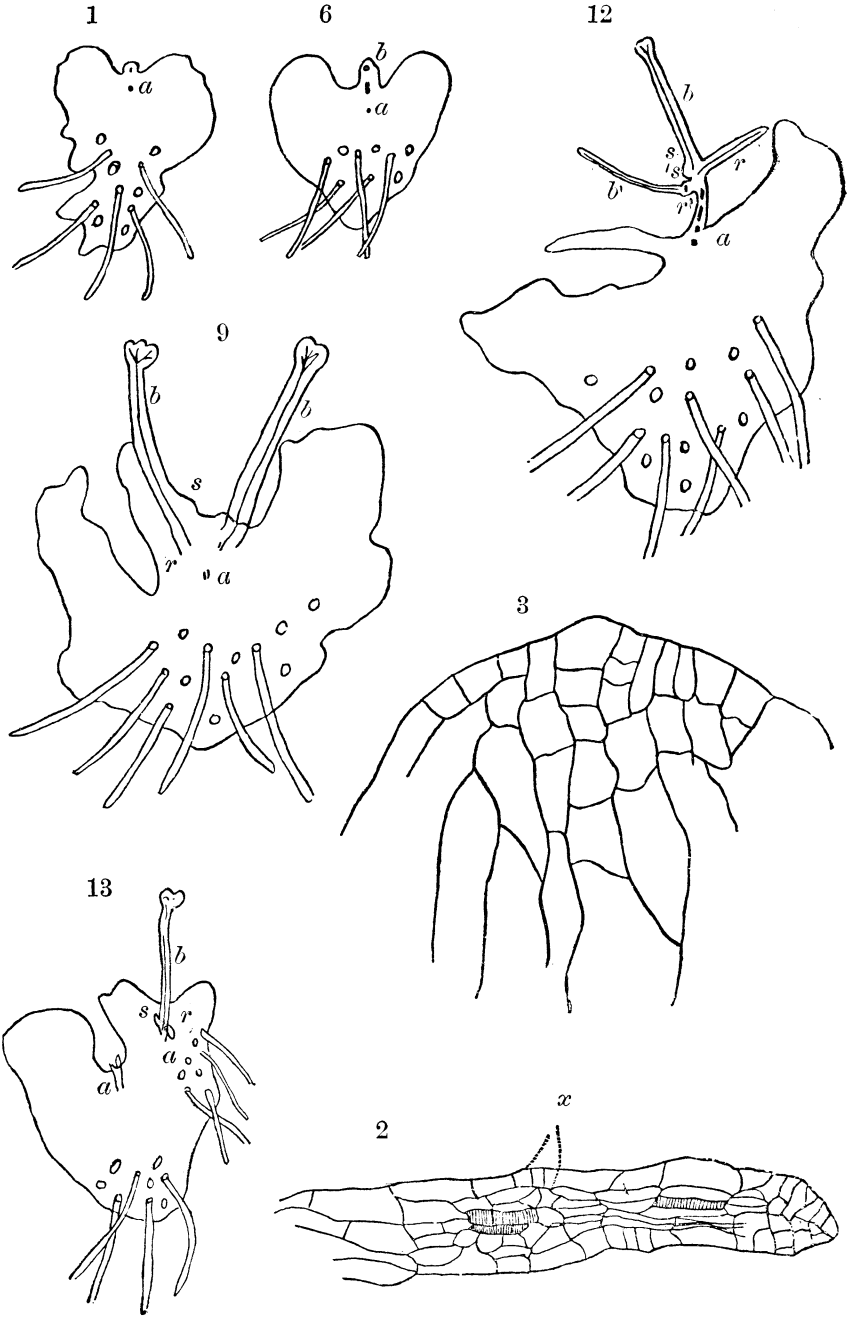
Fig. 8. Portion of a young prothallus, showing the growth in the concavity and scalariform ducts in two groups.

Fig. 10. Magnified view of fig. 9, showing the origins of two leaves and the ducts lying behind in the prothallus.

Fig. 11. Longitudinal section through the place of origin of a young plantlet produced by direct budding: *b* leaf, *r* root, *s* stem-bud, *p*,*p*, prothallus.

Fig. 14. A corresponding section of a normally fertilized prothallus and plantlet, copied from Sachs's Lehrbuch der Botanik: *p*,*p*, prothallus, *f* foot, *d*,*d*, vascular bundle, *b* leaf, *r* root.

Correction. — For PTERIS SERRULATA, in the title and elsewhere, read PTERIS CRETICA. The subsequent development of the plantlets has proved the latter to be the species to which the prothalli belonged. — W. G. F.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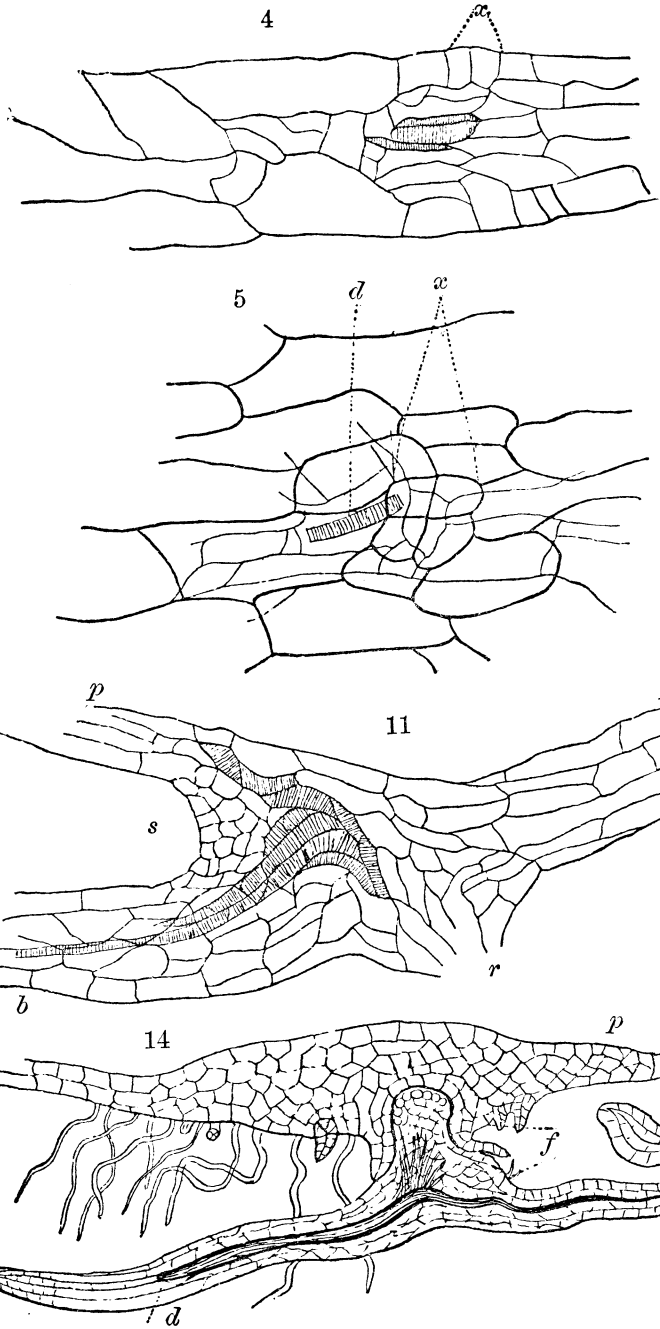
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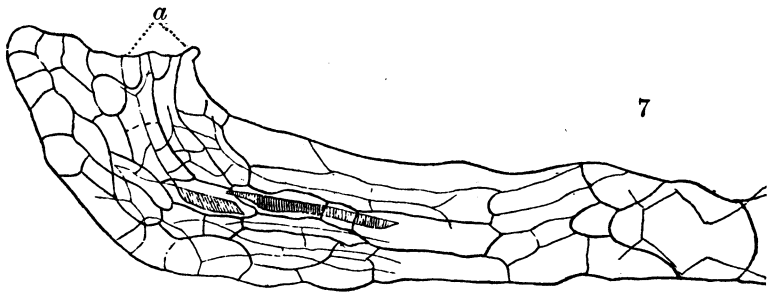

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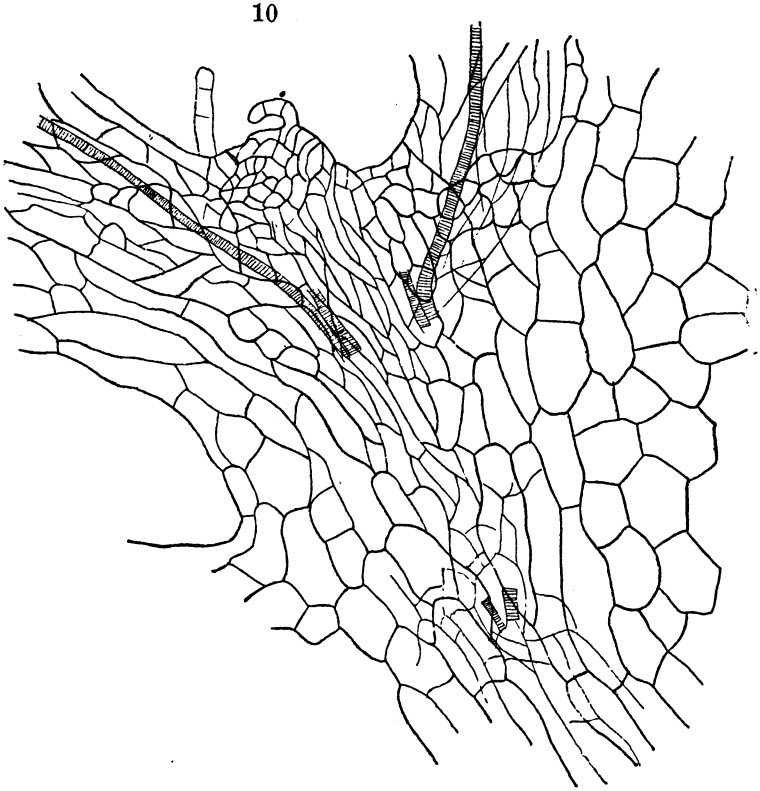

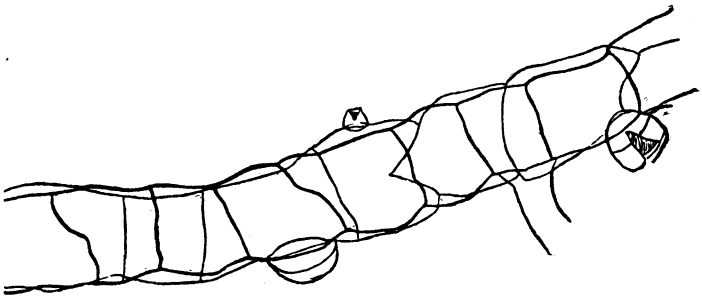

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